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Metabolism of different benthic habitats and their contribution to the carbon budget of a shallow oligotrophic sub-tropical coastal system (southern Moreton Bay, Australia)

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Abstract The major benthic habitats in a shallow oligotrophic sub-tropical coastal system were mapped, benthic productivity and respiration were measured seasonally (summer, winter) in each open water habitat, and an annual carbon budget was constructed using measured, modelled and literature fluxes to estimate the functional importance of each major benthic habitat to the whole ecosystem. Stable *Zostera* Seagrass Communities covered 16% of the open water system but made little contribution to whole system metabolism. In contrast, ephemeral *Halophila* Seagrass Communities covered only 8% of the open water system but contributed 46% of the net productivity (p). The less 'iconic' Inter- and Sub-tidal Pimpama Shoals also only had a small areal extent (10%) but accounted for 50% of the net benthic production. Similarly, Yabby Shoals only covered 27% of the open water system but accounted for 89% of the net respiration (r). Budget estimates suggest that lateral import of organic matter, most likely tidally transported phytoplankton trapped in seagrass beds, across the Broadwater boundaries was required to balance the carbon budget if any reasonable estimate of burial was invoked. However, budget errors make it difficult to distinguish this import from zero. This study demonstrated that shallow subtropical coastal systems have a complex mosaic of benthic habitats, and that some of the less 'iconic' habitats (i.e. non-seagrass, non-mangrove) also make an important functional contribution that controls the flow of energy and nutrients through the whole ecosystem and determines the net ecosystem metabolism and possible exchanges with adjacent systems.

Keywords Benthic microalgae · Carbon · Habitat · Metabolism · Pelagic · Productivity · Seagrass · Budget

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Introduction

Coastal ecosystems are a significant component of the global carbon balance due to intense processing of large inputs of allochthonous and autochthonous organic matter (Borges et al. 2005). Shallow coastal systems (coastal lagoons) typically have smaller catchments and lack the large river systems of larger

deeper estuaries (McGlathery et al. 2007), which would increase the importance of autochthonous and lateral inputs of organic matter (e.g. Santos et al. 2004). The primary production of an ecosystem minus its respiration, or net ecosystem metabolism (NEM), is a measure of how much organic matter is available for higher tropic levels (e.g. fisheries production), burial, and export to adjacent aquatic systems, or, if negative, how much CO_2 is released to the atmosphere and/or exported to adjacent systems. In shallow coastal systems light can reach much of the seafloor and, as such, the majority of this primary production and respiration occurs in the benthos.

Shallow coastal systems typically have a complex mosaic of benthic habitats coupled to pelagic habitats (Ziegler and Benner 1999; Barron et al. 2004). This complexity of benthic habitats is an important factor for determining the diversity and composition of ecological communities (Hosack et al. 2006). It may be the connectivity, and the flow of energy, nutrients and organisms between these functionally different habitats that maintains overall ecosystem function and higher order production (e.g. fish; Cloern 2007). As such, in shallow coastal systems, it is the sum of the net rates of production and respiration in each of the different benthic habitats that primarily determines the amount of organic matter available for higher trophic levels and the linkages (i.e. import and export of organic matter) between these shallow coastal systems and adjacent aquatic systems and the atmosphere.

Numerous benthic metabolism studies in shallow coastal systems have been done in single habitat types such as seagrass (Murray and Wetzel 1987), muddy sub-tidal shoals (Eyre and Ferguson 2005), muddy inter-tidal shoals (Cook et al. 2004), sands with macrofauna (Webb and Eyre 2004a), and permeable sands (Cook et al. 2007). Metabolism studies in shallow coastal non-seagrass systems that include more than one benthic habitat typically compare muds and sands, or shoals and channels, or compare similar habitats along a gradient of interest (e.g. salinity, eutrophication, e.g. McGlathery et al. 2001; Ferguson et al. 2003, 2007; Murrell et al. 2009). In oligotrophic seagrass systems all benthic habitats other than seagrass are typically lumped together as 'unvegetated' (e.g. Moncreiff et al. 1992; Ziegler and Benner 1999; Gazeau et al. 2005; Barron et al. 2006), but these unvegetated sediments may be quite variable (e.g. sands and muds, sub-tidal and inter-tidal, with and without large macro-fauna etc.) with an associated variability in metabolism. Without detailed mapping of all benthic habitats and associated benthic productivity and respiration measurements in each habitat, net ecosystem metabolism estimates may misinterpreted. To our knowledge the metabolism of all major benthic habitats within one coastal system have never been compared and the importance of each of these habitats to carbon flow within the whole ecosystem has never been estimated. This study aimed to map the major benthic habitats in a shallow oligotrophic sub-tropical coastal system, measure oxygen and carbon dioxide primary productivity and respiration in each habitat type, and develop a first-order carbon budget to estimate the importance of each habitat to the whole ecosystem metabolism. It is expected that some of the less 'iconic' habitats (i.e. non-seagrass) will also make an important functional contribution to the flow of energy and organic matter through the whole ecosystem. The relationships between benthic oxygen and carbon dioxide fluxes were also explored to give some insight to the relative importance of oxic, suboxic and anoxic pathways of metabolism.

Study area

The study area covers 37.8 km^2 and is a representative section of open water and mangroves in Southern Moreton Bay on the east coast of Australia (Fig. 1). Protected from the ocean by a barrier island system (South Stradbroke Island), the study area is a complex mosaic of islands, shoals and channels. The open water of the study area is called the Broadwater, except for the Pimpama River Estuary. The Broadwater is a barrier lagoon type of wave-dominated estuary (Roy et al. 2001; Harris and Heap 2003) and the Pimpama River Estuary is a tide-dominated delta (Harris and Heap 2003). The northern section of the Broadwater is well flushed with oceanic water through Jumpinpin and the southern section of the Broadwater is well flushed with oceanic water through the Gold Coast Seaway. Tidal channels are up to 9 m deep in places, but overall the study area is shallow with the open water area averaging just 1.74 m deep at mid-tide. Vertical light extinction coefficients range from 0.68 to 1.2 across the study

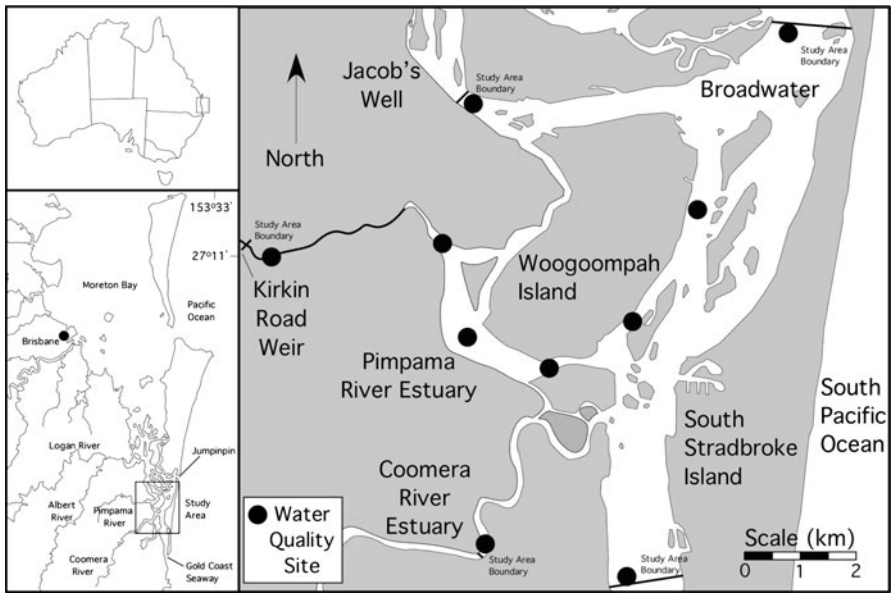


Fig. 1 Location of the southern Moreton Bay study area

area with an average of 0.93 resulting in about 20% of the incident radiation reaching the seafloor. The region receives an average annual rainfall of 1,094 mm (Gold Coast Seaway) with much of it falling in late summer. The Pimpama River Estuary with a catchment of 130 km^2 is the only freshwater input that discharges directly into the study area. However, during large floods the northern section of the study area can be briefly influenced by freshwater from the Logan River and the southern section can be briefly influenced by freshwater from the Coomera River.

Methods

Water quality

Chlorophyll-a samples were collected monthly from July 2003 to June 2004 at 10 sites across the study area ($n = 60$ samples in the Broadwater and $n = 60$ samples in the Pimpama/Coomera River Estuary). Three additional sampling runs were also undertaken immediately following a flood event in February 2004 ($n = 30$). Sampling runs were started mid-flood tide, and were completed within about 2–3 h, allowing all sampling to be completed, as close a possible, on a similar tide phase. Surface samples (top 20 cm) were collected mid-channel using an acid washed and sample rinsed sampling bottle (being careful not to collect the surface scum), and 500–1000 ml of water was immediately filtered through glass fibre filters (Whatman GF/F—0.7 μm nominal pore size) for chlorophyll-a analysis. Each filter was placed into a 10 ml polyethylene vial and wrapped in aluminium foil. A 1000 ml sample was also collected in a sample-rinsed polyethylene bottle for total suspended sediment analysis. Chlorophyll-a was analysed as detailed in Strickland and Parsons (1972). At each sampling site vertical profiles of temperature, salinity and dissolved oxygen were taken at 1 m intervals using a Hydrolab Quanta multi-probe. Secchi disk depth was also measured.

Pelagic productivity

Pelagic productivity was measured at 7 of the water quality sites in March 2004. Additional pelagic productivity measurements were undertaken monthly for 10 months in 2007/2008 at five sites in the lower Richmond River Estuary (see Eyre and Twigg 1997 for location) to develop a more robust pelagic productivity versus chlorophyll-a relationship for use in the carbon budgeting. Water from each site was placed in nine 250 ml BOD bottles. Triplicate light bottles, triplicate dark bottles (placed in light-proof calico bags), and triplicate blanks (0.45 μM filtered water) were incubated mid-water column at their respective sites from approximately 8:00 to 16:00 hours. Dissolved oxygen was measured electrochemically (YSI 5000 BOD probe, ±0.01 mg l^{-1})

in each bottle before and after the incubation. Gross pelagic productivity equals the change per unit of time in DO in the light bottle minus the change per unit of time in DO in the dark bottle minus the change per unit of time in DO in the blank bottle.

Habitat mapping

The major benthic habitats in the study area were identified using a combination of aerial photography interpretation with ground-truthing, hydrosurveys (depth) and hydrodynamic modelling. Rectified 1:10,000 colour aerial photography taken in 2003 was used to map areas of mangroves, seagrass (*Zostera*) and shoals and this information was transferred into a GIS data base. Seagrass distributions (*Zostera capricorni*, *Halophila ovalis*, *Halophila spinulosa*) and sandy Yabby Shoals (burrowing shrimp, *Trypaea australiensis*) were ground-truthed by visually mapping the edges by snorkelling and differential GPS at low tide. The sub-tidal and inter-tidal shoals and deep channels were mapped using detailed hydrosurveys (±0.01 m). The null zone channel was defined by hydrodynamic modelling (Szylkarski et al. 2005; SKM 2006) as an area of low current velocities and visually in cores as an area where phytodetritus accumulated. The Pimpama habitats were defined geographically as part of the Pimpama river estuary system. The upper Pimpama was defined on the basis of depth (>3 m at high tide) and visually in cores as an area where phytodetritus accumulated. A 5% measurement error was adopted for surface area and volume estimates (Eyre 1995).

Thirteen habitat types were identified within the study area (Fig. 2). Four of the habitats were not considered in detail because of their small areal extent [i.e. Couran Cove (0.1 km^2): a man made canal estate; organic muds (0.2 km^2): old seagrass (*Zostera capricorni*) areas; Pimpama Channel (0.1 km^2)] and because the hard bottom could not be sampled with cores or chambers (Broadwater Channel (1.0 km^2): scoured by high velocity currents). Benthic process measurements were undertaken in 8 of the 9 remaining major habitats (all the open water habitats) and mangrove productivity and respiration were estimated using rates measured just north of the study area (Dennison and Abal 1999). These nine major habitats cover 96.6% of the study area (Table 1).

Benthic biogeochemical process measurements

Benthic production and respiration were measured in triplicate in winter (July 2003) and summer (January 2004) in all the open water habitats (see Table 1). Sampling was undertaken in summer and winter because maximum benthic productivity and respiration in sub-tropical coastal systems typically occurs in summer, and minimum benthic productivity and respiration typically occurs in winter (Eyre and Ferguson 2005). Benthic chambers were used in the Yabby Shoals and *Zostera capricorni* Seagrass Communities, as the important structural elements of these habitats could not be captured in cores. Undisturbed cores were used in the other benthic habitats. We recently compared core and chamber incubations on an inter-tidal shoal over an annual cycle and found no significant ($p < 0.05$) difference in net production between the two incubation devices (Damien Maher, unpublished data). The good relationship between Gross O_2 Productivity and Gross CO_2 Fixation across all habitats in both seasons (see "Discussion") further indicates that there is no systematic bias in measured rates associated with using two types if incubation methods. Core measurements were taken over a complete 24 h diel cycle, in summer (14 h of light; 10 h of dark) and winter (10 hours of light; 14 hours of dark). Chamber measurements were undertaken over a 3–4 h period. Light rates were corrected to account for differences in phytosynthetically active radiation (PAR) received during the short incubation period compared to the whole day (i.e. cores). PAR was logged every minute from sunrise to sunset using a Li-Cor 250 meter with a 2-pi sensor.

Triplicate sediment cores (approximately 20 cm long) including overlying water (approximately 2.3 l) were collected from the 6 benthic habitats in 500 mm long, 90 mm I.D. clear acrylic pipes using a hand operated surface corer. Cores were examined to ensure that the bulk of the sediment surface was intact. Cores were shaded and transported to the incubation site at Jacobs Well (Fig. 1). Incident radiation (2 pi) was measured at the top and bottom of the water column at the sample site using a Li-Cor 250 light meter to determine light attenuation. A Teflon stir bar was suspended approximately 10 cm from the sediment surface of each core and cores were submerged in an incubation tank containing approximately 100 l of site water at in situ

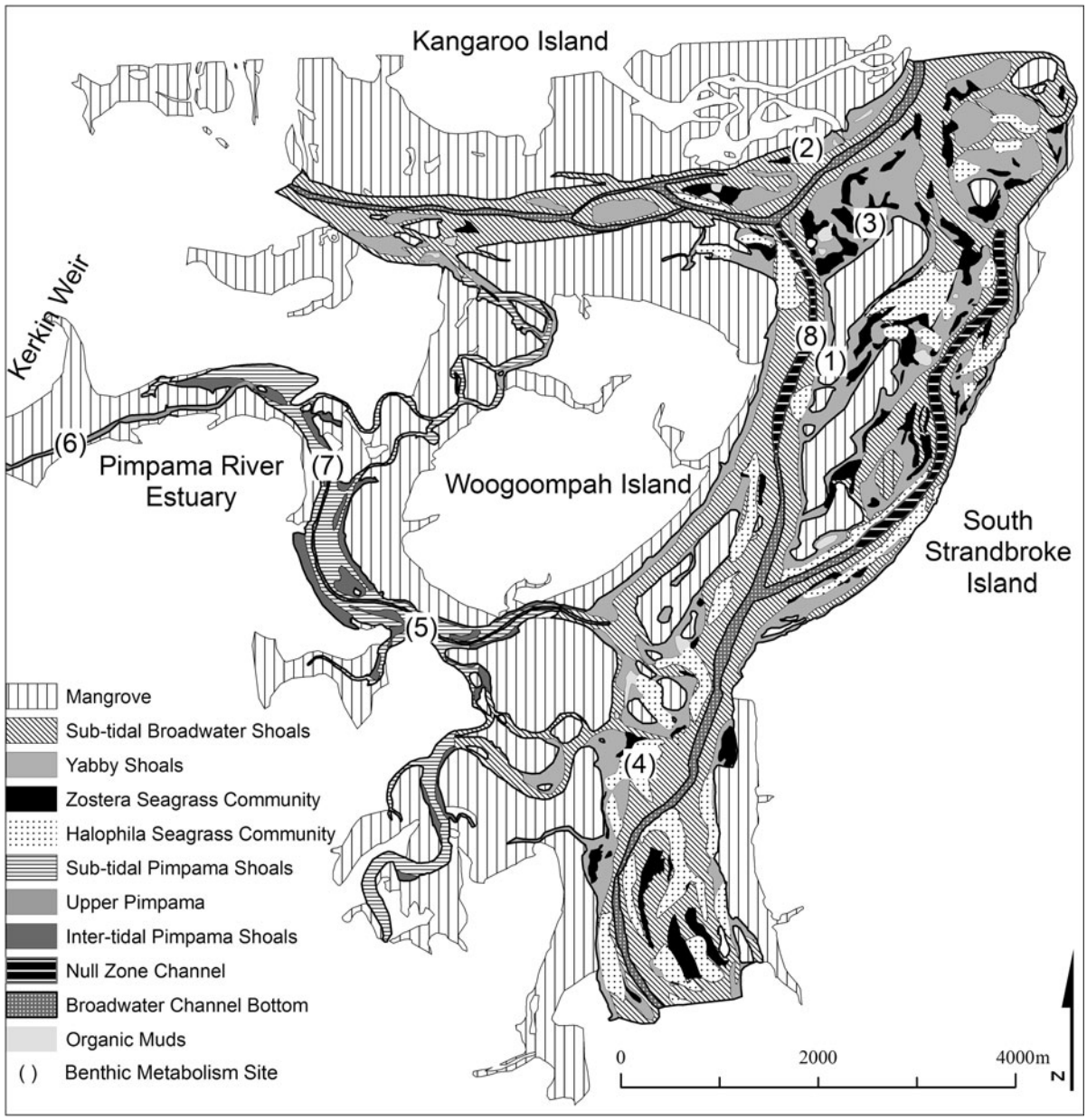


Fig. 2 Benthic habitat map of the southern Moreton Bay study area

temperature (±1°C) and natural light (±5.0%). The stirring rate was adjusted to just below the threshold for re-suspension. Cores were left uncapped to allow free exchange of water for the first 24 h, allowing solute concentrations to equilibrate. At sunset following the 24-hour equilibration period, cores were sealed with clear Plexiglas lids to commence the incubation. The first sample was taken approximately 2 h after closing the cores to allow the partial pressure and concentration of O_2 to drop below 100% saturation (to stop bubbles forming in N_2/Ar samples). Dissolved oxygen concentrations (±0.01 mg l^{-1}) and pH (±0.001 pH units) were measured electro-chemically at 0, 3, 10/12 h during the dark cycle and 0 (i.e. dawn), 2, 4 and 14/12 h during the light cycle. The light cycle followed directly from the dark cycle without uncapping the cores to allow at least a second light N_2/Ar sample to

Table 1 Areal extent of the eight major benthic habitats in the Southern Moreton Bay study area

Habitat	Area (km^2)	Area (%)
Open water		
Sub-tidal Broadwater Shoals	6.5 ± 0.3	17.2
Yabby Shoals	5.4 ± 0.3	14.3
Zostera Seagrass Community	3.2 ± 0.2	8.5
Halophila Seagrass Community	1.7 ± 0.1	4.5
Sub-tidal Pimpama Shoals	1.5 ± 0.1	4.0
Upper Pimpama	0.9 ± ≤0.1	2.4
Inter-tidal Pimpama Shoals	0.6 ± ≤0.1	1.6
Null Zone Channel	0.4 ± ≤0.1	1.1
Open water total	20.2 ± 1.0	53.6
Mangrove	16.3 ± 0.8	43.0
Study area total	36.5 ± 1.8	96.6

be collected before the core water column became saturated. As a sample was withdrawn, an equal amount was replaced from a gravity-fed reservoir of site water. Nutrient and N_2/Ar samples were also collected but this data is reported elsewhere (Eyre et al. 2010). Upon completion of the core incubations benthic chlorophyll-*a* samples were taken by scraping 1 cm^3 samples from the top 2 mm of sediment (i.e. 5 cm^2) and placing these into pre-filled (90% acetone) 15 ml centrifuge tubes. These samples were sealed, wrapped in foil and kept at −20°C until analysis. A 30 g solid phase sample from the upper 20 mm of sediment was also taken and stored frozen for total organic carbon analysis. Details of the sediment chlorophyll-a and organic carbon analytical methods are detailed in Eyre and Ferguson (2002).

Benthic chamber incubations were done over four consecutive days during high tide using triplicate transparent acrylic benthic flux chambers (290 × 290 × 200 mm deep—approximate volume 16.8 l, see Webb and Eyre 2004b for details). Light (day) and dark (night) incubations were undertaken in representative populations of marine yabbies (*Trypaea australiensis*; 80–100 m^{-2}) over the first 2 days and in the *Zostera* Seagrass Community during the last 2 days. Four samples were withdrawn from the chambers over a 210 min incubation period. The first 60 ml of water drawn from the remote sample tubes of each chamber was discarded (60 ml = volume of sample tubes plus 20% extra for tube flushing). A 150 ml sample vessel with probe ports was then filled from each chamber and dissolved oxygen (YSI 5000 BOD probe, ±0.01 mg l^{-1}), pH and temperature (Denver AP25 pH probe, ±0.001) were recorded. Nutrient and N_2/Ar samples were also collected (reported in Eyre et al. 2010). At the end of the chamber incubations cores were collected from within the chambers and sampled for chlorophyll-a and organic carbon as detailed above.

Fluxes across the sediment–water interface were calculated by linear regression of the concentration data, corrected for the addition of replacement water and the blank as a function of incubation time, core water volume and surface area. Dark flux rates were calculated using concentration data from the night-time and light flux rates from the day-time part of the incubation. To allow comparison of chamber rates and core rates and to allow system-wide scaling of the fluxes, light rates for the chamber incubations were corrected for the total amount of light received during the incubation compared to the total amount of light received during the whole day (about 50%). The following parameters were calculated from the dark and light rates (sign denotes dominant flux direction).

$$\text{Gross benthic carbon fixation } (-\text{ve, uptake}) = \text{Light } TCO_2 \text{ flux } (-\text{ve}) - \text{Dark } TCO_2 \text{ flux } (+\text{ve})$$

$$\text{Gross benthic oxygen production } (+\text{ve, efflux}) = \text{Light } O_2 \text{ flux } (+\text{ve}) - \text{Dark } O_2 \text{ flux } (-\text{ve})$$

$$\text{Benthic } TCO_2 \text{ p/r} = \text{gross } TCO_2 \text{ fixation} \times \text{daylight hours/dark } TCO_2 \text{ flux} \times 24 \text{ h}$$

$$\text{Benthic } O_2 \text{ p/r} = \text{gross } O_2 \text{ productivity} \times \text{daylight hours/dark } O_2 \text{ flux} \times 24 \text{ h}$$

$$\text{Benthic dark respiratory quotient (RQ)} = \text{dark } TCO_2 \text{ flux: dark } O_2 \text{ flux}$$

Statistical analysis

For water quality, two-way analyses of variance (ANOVAs) were run in SPSS (version 17.0) to test differences between sites (Broadwater, Pimpama) and season (summer, winter, post-flood). Two-way analyses of variance (ANOVAs) were also run for benthic respiration and productivity rates to test differences among the eight open water habitats and between seasons (summer, winter) and for interacting effects

of site and season. The significance level (alpha) was specified as 0.05. Levene's test showed in some cases that variances in the compared groups were heterogeneous. Presence of negative values in the data set prevented log transformation to improve homogeneity of variances. However, provided that sample sizes are similar, as was the case for most of the tests undertaken, ANOVAs are robust to violations of the assumption of homogeneous variances (Zar 1999). The chance of a type I error (falsely identifying a significant difference) was also further reduced by defining the significance level as 0.01 when Levene's tests were violated. One-way ANOVAs were used to further investigate the component parts where there was an interaction with the effect of season dependent on site. The effect of site was investigated separately for summer and winter, and the effect of season was investigated separately for each site. Where significant differences were found using two-way and one-way ANOVAs, post hoc Tukey tests were used to determine which sites or seasons had similar or different respiration and productivity rates.

Carbon (C) budgets

To illustrate the functional importance of each of the benthic habitats to the whole ecosystem, carbon budgets were estimated for the whole study area using the C modelling framework of Eyre and McKee (2002). The budget modelling assumes steady state, therefore the sum of inputs, outputs and storage of carbon within the defined system should equal zero ± error. The model includes four major inputs for carbon (1) diffuse (Pimpama River), (2) lateral (Logan and Coomera River during flooding), (3) atmospheric deposition, and (4) primary production. Outputs of carbon include (1) burial, (2) fisheries harvest, and (3) exchange through the Broadwater boundaries and (4) CO_2 loss to the atmosphere. Standing stocks include (1) dissolved organic carbon in the water column, (2) solid phase sediment carbon, and (3) floral biomass (mangroves, seagrasses, benthic microalgae and phytoplankton).

Spatial and temporal boundaries, nutrient speciation, units of mass, significant figures and errors

The carbon budget boundaries are given in Fig. 2. The carbon budget was developed for one year (July 2003 to June 2004). Mass (tonnes (t) = 10^3 kg) was used throughout all calculations. All terms were rounded to 0.1 t (100 kg), even though the accuracy this suggests is much greater than can be justified by the methods used. This was to avoid progressive accumulation of rounding errors and to avoid loss of some of the smaller fluxes, which were less than the rounding errors of the larger fluxes. Budget errors were assessed in three ways. Firstly, errors were assigned to each of the budget terms that were the product of two terms (e.g. benthic carbon production = benthic rate of production × area) using the following formula (modified from Eyre 1995):

$$\text{Budget term error} = \Big((\text{mean}_1 \times \text{error}_2)^2 + (\text{mean}_2 \times \text{error}_1)^2 + (\text{error}_1 \times \text{error}_2)\Big)^{0.5}$$

Errors are given for each data set. Secondly, a sensitivity analysis was done where each of the terms in the budget (e.g. overall burial rates) were adjusted up and down by their estimated errors to determine if the overall conclusions derived from the budget changed. When the productivity errors were applied the corresponding respiration errors were also applied, to calculate the errors in the budget surplus/deficit (Net Broadwater Exchange). Thirdly, a 'convergence of multiple estimates' approach (Kemp et al. 1997; Eyre and McKee 2002) was used where some of the budget terms were verified by independent measures.

Diffuse and lateral catchment loads and atmospheric loads

Total diffuse and lateral catchment organic carbon (TOC) loads were estimated using the total nitrogen loads from Eyre et al. (2010) and a mass TOC/TN ratio of 11.2:1 (Eyre and McKee 2002). Errors associated with the diffuse carbon loads are difficult to quantify because the nitrogen loads were modelled. As such a 100% error was assigned to the diffuse carbon loads. Atmospheric deposition loads were estimated using rainfall concentration data for coastal northern NSW 200 km south of the study area (McKee and Eyre 2001), mean annual rainfall for the study area (Gold Coast Seaway = 1094 mm) and the total surface area of the study area (37.8 km^2). The northern NSW rainfall concentration data were from coastal sites and therefore represent similar

conditions to the study area (i.e. clean air sourced from the Pacific Ocean). No dry fall data was available. As such, the wet fall loads were multiplied by 1.2, the ratio of total nitrogen deposition (wet + dry) to wet nitrogen deposition for the South Pacific Ocean (Paerl 1995). The same ratio was assumed to apply for phosphorus. Errors associated with the atmospheric carbon loads are difficult to quantify because the concentration data were derived from coastal northern NSW. As such a 100% error was assigned to the atmospheric carbon loads.

Carbon production

Pelagic productivity was estimated using measured monthly chlorophyll-a concentrations at each site, a chlorophyll-a biomass/productivity relationship (see Fig. 3), and a photosynthesis quotient of 1.2 (Laws 1991). The estimated pelagic productivities for each month were multiplied by the volume of water around each of the chlorophyll-a sites. The volumes were determined from detailed hydrographic surveys and a digital elevation terrain model, which was incorporated into a hydrodynamic model of the study area (Szylkarski et al. 2005; SKM 2006). Benthic productivity for each of the open water benthic habitats was estimated by multiplying the average of the measured hourly summer and winter gross productivities by the hours of daylight in each season, by 365 days for each habitat, by its surface area. The standard deviation of the triplicate benthic and pelagic productivity measurements was adopted as the error for the rate measurements. For the whole ecosystem budget, all the open water habitats that did not contain seagrass were grouped together for the benthic microalgae productivity. The four minor habitats (see results) were excluded. Mangrove biomass estimates, and litter fall estimates of mangrove productivity, have been made in Moreton Bay just north of the study area (see Fig. 1; Dennison and Abal 1999). The Moreton Bay ratios of mangrove biomass/productivity from Dennison and Abal (1999) were applied to mangrove biomass measurements in the study area (SKM 2006) to estimate mangrove productivity. Litterfall estimates can underestimate mangrove production by up to 50% (Clough et al. 1997) and as such, an error of 100% was adopted.

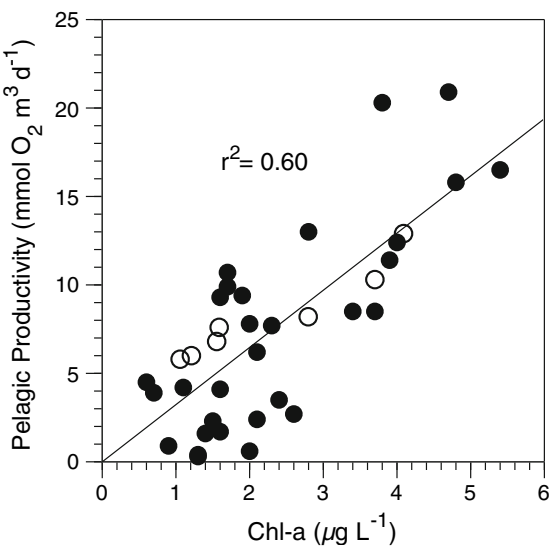


Fig. 3 Pelagic productivity versus chlorophyll-a for the southern Moreton Bay study area and the subtropical lower Richmond River Estuary

Carbon burial and respiration (carbon loss)

Carbon burial was estimated for the whole study using average burial rates for mangrove and seagrass communities and non-vegetated estuarine sediments (Duarte et al. 2005) and their areal extent. Errors associated with carbon burial are difficult to quantify because literature values were used. As such a 100% error was assigned to carbon burial. Pelagic respiration was determined from the measured respiration rates assuming respiration quotient of 0.8 (Laws 1991). Benthic respiration was estimated for each open water benthic habitat by multiplying the average of measured hourly winter and summer benthic respiration rates by 24 h, by 365 days in each habitat, by its area. The standard deviation of the triplicate benthic and pelagic respiration measurements was adopted as the error. It was assumed that 78% of the mangrove production was lost through plant and heterotrophic respiration (Alongi 1998).

Fisheries harvest

There is no commercial fishing within the study area. The harvest of fish by recreational fishers was estimated by applying the areal recreational catch for Moreton Bay just north of the study area (Eyre and McKee 2002) to the water surface area of the study area. Dry weight was assumed to be 20% of the

wet catch and the carbon content of the dry catch to be 50% (Eyre and McKee 2002). Errors associated with fisheries harvest are difficult to quantify because values from Moreton Bay were used. As such a 100% error was assigned to fisheries harvest.

Broadwater exchange

When all the inputs and outputs were added the Broadwater exchange of carbon (including the northern and southern Broadwater, Coomera and Jacobs Well boundaries) was calculated by difference; +ve = an export and −ve = an input. This term also includes the sum of the errors associated with the other components of the budget.

Standing stocks

Carbon standing stocks in the water column were estimated by applying water column total nitrogen concentrations in the study area (Eyre et al. 2010) by carbon: nitrogen ratios for Moreton Bay (connected main water body just north of the study area, see Fig. 1; Eyre and McKee 2002). Solid phase carbon pool sizes in the study area were estimated by multiplying the average of measured winter and summer sediment organic carbon concentrations in each habitat by the area of each habitat by 20 mm. An arbitrary depth of 20 mm was adopted as this material is probably still biogeochemically active within the system, and it was the depth of sediment sampled in the cores and chambers. Carbon stocks in the biomass of mangroves, seagrasses and benthic microalgae (BMA) was estimated by multiplying the measured biomass of each flora group by their measured areal extent (Burch and Tomey 2005; SKM 2006).

Results

Water column physico-chemical parameters, chlorophyll-a and pelagic productivity

During summer and winter mean salinity in both the Broadwater and Pimpama/Coomera River Estuary approached seawater, reflecting the rapid tidal flushing across the system (Table 2). Following floods, salinity can briefly drop 10–15 in the Broadwater and to near zero in the Pimpama/Coomera River Estuary.

Table 2 Water quality in the southern Moreton Bay study area

	Pimpama/Coomera summer ($n = 36$)		Pimpama/Coomera winter ($n = 24$)		Pimpama/Coomera post-flood ($n = 18$)		Broadwater summer ($n = 24$)		Broadwater winter ($n = 16$)		Broadwater post-flood ($n = 12$)	
	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
Salinity	36.0 ± 0.5	19.3–39.3	34.6 ± 0.5	25.3–36.8	18.2 ± 2.6	0.4–31.6	36.5 ± 0.2	34.2–37.4	35.8 ± 0.2	34–36.7	27.8 ± 1.5	19.4–34.8
Temperature (°C)	24.1 ± 0.6	19.5–30.8	19.2 ± 0.3	17.4–21.7	29 ± 0.3	27.1–31.1	22.9 ± 0.6	18.6–28.3	18.9 ± 0.3	17.2–20.6	27.6 ± 0.3	25.5–29.6
O_2 (% sat)	90.3 ± 1.5	67–108.6	88.8 ± 1.7	65.5–101.1	79.6 ± 5.4	14.2–113.4	94.6 ± 0.9	86.7–103.9	92.1 ± 0.8	87.3–98.3	92.1 ± 3.0	80.5–107.4
Secchi (m)	1.0 ± 0.1	0.5–2.0	1.3 ± 0.1	0.7–2.0	0.5 ± 1.0	0.1–0.8	1.3 ± 0.2	0.4–4.0	1.6 ± 0.2	0.7–3.2	0.7 ± 0.1	0.4–1.1
TSS (mg l^{-1})	20.6 ± 1.1	14.2–44.2	14.0 ± 0.6	8.7–19.6	25.2 ± 3.4	8.5–75.3	21.8 ± 2.0	11.9–51.7	15.1 ± 0.8	7.9–21	21.9 ± 1.7	14.2–36.9
Chl a (μg l^{-1})	2.6 ± 0.5	0.3–13.9	1.9 ± 0.2	0.6–4.4	9.3 ± 3.3	1.1–57.2	1.8 ± 0.4	0.2–7.4	1.4 ± 0.2	0.6–2.9	5.0 ± 0.8	2.5–11.1

Summer is the average of samples collected at 10 sites in September, October, November, December, January and April. Winter is the average of samples collected at 10 sites in May, June, July and August. Post-flood is the average of samples collected at 10 sites twice in February and in March, in 2003 and 2004

Mean dissolved oxygen concentrations are near saturation across the study area in winter and summer but drop significantly ($F = 11.485$; $p < 0.001$; $df = 2,124$) following floods in the Pimpama/Coomera. Water temperatures across the system were typical for a sub-tropical climate ranging from about 17 to 31°C. Total suspended sediment concentrations were significantly higher in summer and post-flood than winter ($F = 6.954$; $p < 0.001$; $df = 2,124$) with concentrations up to 75.3 mg l^{-1} measured in the Pimpama/Coomera River Estuary following the February flood. Secchi depths averaged 1.1–1.4 m across the system but can be as deep as 4.0 m on the flood tide when clear oceanic water intrudes into the Broadwater. Secchi depths were significantly different between seasons ($F = 28.000$; $p < 0.001$; $df = 2,124$) with the highest depths in winter and the lowest post-flood. There was no significant difference in chlorophyll-a concentrations between summer and winter and between the Broadwater and Pimpama/Coomera River Estuary in summer and winter. Following floods, diffuse loads of dissolved inorganic nitrogen from the catchment (Eyre et al. 2010) can stimulate phytoplankton growth in the Coomera and upper Pimpama river estuaries with recorded chlorophyll-a concentrations up to 57.2 and 33.1 μg l^{-1} respectively.

Pelagic productivity in the study area ranged from 5.8 to 12.9 mmol O_2 m^{-3} day^{-1} and was strongly correlated with chlorophyll-a concentrations ($r^2 = 0.91$; $p < 0.01$; $n = 7$). The pelagic productivity versus chlorophyll-a relationship for the study area closely matched the larger data set from the Richmond River Estuary 200 km south of the study area (Fig. 3). Combining the two data sets gave the following significant relationship ($r^2 = 0.60$; $p < 0.001$; $n = 36$):

$$\text{Pelagic productivity}\left(\text{mmol } O_2\ m^{-3}\ day^{-1}\right) = 3.24 \times \text{chlorophyll-a}\left(\mu g\ l^{-1}\right)$$

Areal extent and description of major benthic habitats

Open water habitats in total covered about 53.6% of the study area (Table 1). Mangroves were the largest individual habitat and covered 43% of the study area (Table 1). *Avicennia marina*, *Bruguiera gymnorrhiza* and *Aegiceras corniculatum* were the dominant mangrove species. The Sub-tidal Broadwater Shoals had the second largest areal extent (17%) and consisted of fine sands and muds with a surface layer of benthic microalgae. The Yabby Shoals covered 14% of the study area and were inter-tidal fine sands with yabby burrows (burrowing shrimp—*Trypaea australiensis*) at a density of up to 400 m^{-2} (average 80–100 burrows m^{-2}). The remaining habitats individually covered <10% of the study area. *Zostera capricorni* Seagrass Communities covered 8.5% of the study area and represent quite permanent features with most of the beds having had a similar areal extent for the past 30 years (SKM 2006). In contrast, the *Halophila ovalis* and *Halophila spinulosa* seagrass communities were ephemeral with the distribution shown in Fig. 2 representing an average coverage. The seagrass blades on the three dominant species all had a light cover of epiphytes and the sediment between the seagrass had a cover of benthic microalgae. The Null Zone Channel is a low tidal energy area where oceanic water flowing in from Jumpinpin (north) and the Gold Coast Seaway (south) meet, resulting in the deposition of muds and phytodetritus. The Upper Pimpama (average 3 m depth) is the narrow poorly flushed upper section of the Pimpama River Estuary and is separated from the remainder of the estuary by a shallow (<0.5 m at low tide) sub-tidal shoal. Fine organic rich muds with a thick layer of phytodetritus were characteristic of this habitat. The Sub-tidal Pimpama Shoals had a similar areal extent to the *Halophila* Seagrass Communities (about 4%) and were similar to the Sub-tidal Broadwater Shoals, except that they were covered with a thick layer of filamentous algae. The Inter-tidal Pimpama Shoals were mostly fine muds with a cover of benthic microalgae and only covered a small percentage (<2%) of the study area.

Sediment organic carbon and chlorophyll-a

The highest winter organic carbon (OC) concentrations were in the upper Pimpama (3404 μmol g^{-1}), followed by the Inter-tidal Pimpama shoals (1787 μmol g^{-1}), Subtidal Broadwater Shoals (1332 μmol g^{-1}), Null Zone Channel (1301.4 μmol g^{-1}), Sub-tidal Pimpama (1028 μmol g^{-1}), *Zostera* Seagrass Community (779 μmol g^{-1}), *Halophila* Seagrass Community (589.8 μmol g^{-1}) and, finally, the Yabby Shoals (482 μmol g^{-1}; Fig. 4a). There was a significant difference between seasons depending on site (2-way interaction: $F = 21.580$; $p < 0.001$; $df = 7,9$) with

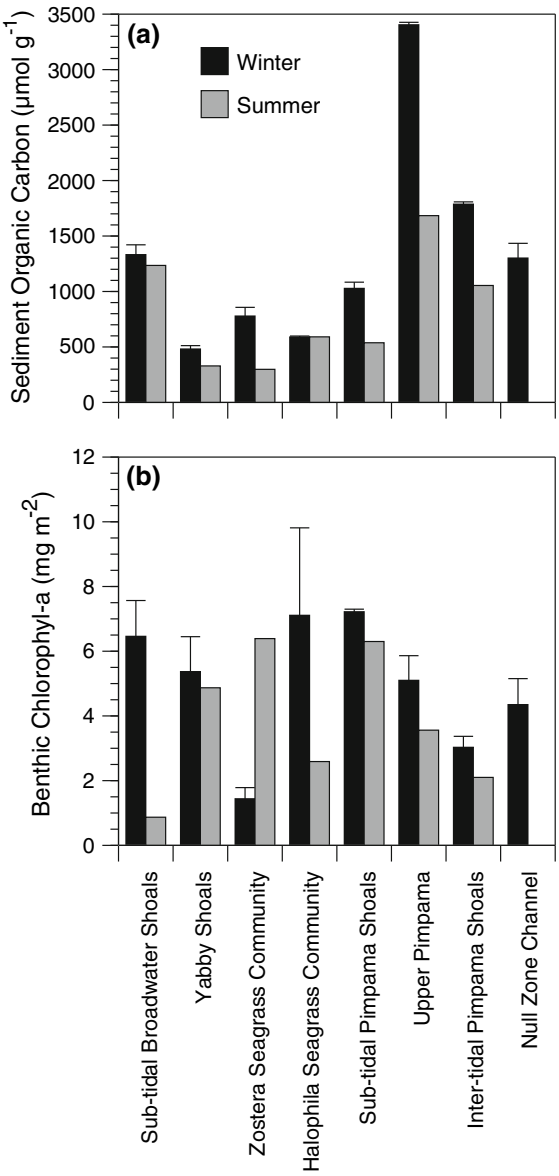


Fig. 4 Sediment **a** organic carbon concentration and **b** chlorophyll-a concentrations in the eight open water benthic habitats in the southern Moreton Bay study area. Winter (Mean ± SE; $N = 3$); Summer ($n = 1$)

significantly lower OC concentrations during summer at all Pimpama River Estuary sites, as well as the *Zostera* Seagrass Community and Yabby Shoals. The spatial pattern of OC across the study area was similar during both seasons. In general, OC increased with mean water depth ($r^2 = 0.41$), reflecting the role of deeper sites as depositional areas.

The highest sediment chlorophyll-a concentrations occurred in winter in the *Halophila* Seagrass Community, Sub-tidal Pimpama Shoals and Sub-tidal Broadwater Shoals (~6 to 7 mg m^{-2}). The highest sediment chlorophyll-a concentrations in summer were slightly lower than in winter and occurred in the Sub-tidal Pimpama Shoals, *Zostera* Seagrass Community and Yabby Shoals. Sediment chlorophyll-a concentrations in the Yabby Shoals, Sub-tidal Pimpama Shoals, Upper Pimpama and Inter-tidal Pimpama Shoals showed little change between summer and winter, while the other habitats, particularly the seagrass communities, showed a much larger change.

Benthic respiration

Dark fluxes of TCO_2 during winter ranged from 225 to 2461 µmol m^{-2} h^{-1} with the highest rates in the Sub-tidal Pimpama and Yabby Shoal habitats (Fig. 5). Despite this range in respiration rates there was no significant difference across the study area during winter due to high intra-site variability. Dark fluxes of TCO_2 during summer ranged from 469 to 10539 µmol m^{-2} h^{-1} with significantly higher rates in the *Zostera* Seagrass Community and *Halophila* Seagrass Community ($F = 6.079$; $p = 0.002$; df = 7,14). There was a significant increase in respiration from winter to summer in the Sub-tidal Broadwater Shoals ($F = 68.465$; $p = 0.004$; df = 1,3), *Zostera* Seagrass Community ($F = 11.435$; $p = 0.043$; df = 1,2), *Halophila* Seagrass Community ($F = 17.089$; $p = 0.026$; df = 1,3) and Null Zone Channel ($F = 44.055$; $p = 0.007$; df = 1,3). In contrast, there was a significant decrease in summer respiration at the Sub- and Inter-tidal Pimpama Shoals probably due to the noticeably sparser cover of filamentous benthic microalgae (personal observation) and decreased benthic production (and hence labile carbon supply) at these sites compared to winter.

Dark O_2 fluxes showed the same general pattern as dark TCO_2 fluxes with a significant increase from winter to summer in Sub-tidal Broadwater Shoals ($F = 35.812$; $p = 0.009$; df = 1,3) *Zostera* Seagrass Community ($F = 14.460$; $p = 0.032$; df = 1,3), *Halophila* Seagrass Community ($F = 38.571$; $p = 0.008$; df = 1,3) and Null Zone Channel ($F = 66.272$; $p = 0.004$; df = 1,3), but also in the Yabby Shoals ($F = 23.522$; $p = 0.005$; df = 1,5) and Inter-tidal Pimpama Shoals ($F = 49.533$; $p = 0.006$; df = 1,3). The highest O_2 respiration rates in summer were in the *Zostera* Seagrass Community but, unlike TCO_2

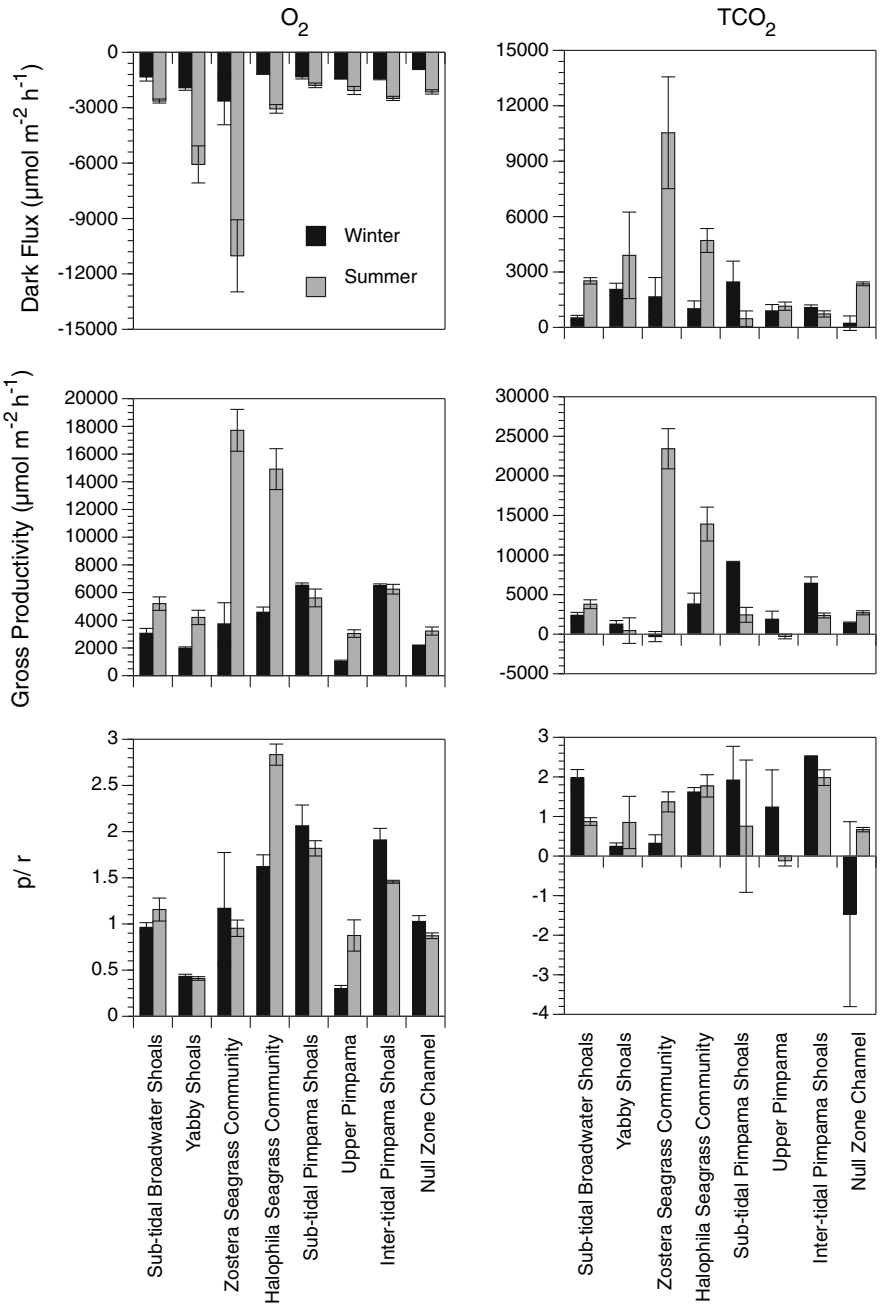


Fig. 5 Winter and summer dark TCO_2 and O_2 fluxes (respiration) (mean ± SE; $n = 3$), gross TCO_2 and O_2 productivity (mean ± SE; $n = 3$), and gross productivity/respiration (p/r) ratios (mean ± SE; $n = 3$) for the eight open water benthic habitats

respiration, the second highest summer O_2 respiration rates were in the Yabby Shoals (Fig. 5).

Benthic gross productivity

All sites had benthic O_2 production during the light, with the highest rates during winter at the Sub- and Inter-tidal Pimpama Shoals (6534 and 6502 µmol O_2 m^{-2} h^{-1}; Fig. 5). There was a significant increase in benthic gross O_2 production from winter to summer at all sites except the Sub-tidal and Inter-tidal Pimpama Shoals. The largest seasonal increase in benthic gross O_2 production was for the *Zostera* and *Halophila* Seagrass Communities. Benthic gross TCO_2 fixation showed a similar pattern to gross O_2 production with an increase from winter to

summer with the highest rates in the seagrass communities but the seasonal increases were not significant in the Sub-tidal Broadwater Shoals, Yabby Shoals and Upper Pimpama. Overall benthic gross TCO_2 fixation and gross O_2 production rates were strongly correlated ($r^2 = 0.87$; $p < 0.001$; $n = 16$) although gross TCO_2 fixation showed a greater variation between seasons than gross O_2 production, particularly at Sub- and Inter-tidal Pimpama Shoals.

Benthic productivity/respiration (p/r) is a measure of the balance between autotrophic production and heterotrophic respiration in the benthic communities. The Yabby Shoals and Upper Pimpama were net O_2 heterotrophic, the Halophlila Seagrass Communities, Sub- and Inter-tidal Pimpama Shoals were net O_2 autotrophic and the *Zostera* Seagrass Communities and Channel Null Zone had near balanced O_2 p/r (Fig. 5). Only the *Halophila* Seagrass Community ($F = 47.680$; $p = 0.006$; df = 1,3) and Inter-tidal Pimpama ($F = 22.602$; $p = 0.018$; df = 1,3) showed a significant seasonal change in O_2 p/r, reflecting a similar seasonal change in both gross O_2 productivity and respiration in the other habitats. Only the Sub-tidal Broadwater Shoals, *Zostera* Seagrass Community and Inter-tidal Pimpama Shoals showed a seasonal change in TCO_2 p/r. Overall O_2 and TCO_2 p/r were not well correlated ($r^2 = 0.21$; not significant; $n = 16$) due to the differences in the two measures of respiration (see "Discussion"). O_2 p/r decreased with increasing depth across the study area ($r^2 = 0.33$; not significant; $n = 14$; Yabby Shoals excluded) and TCO_2 p/r ($r^2 = 0.44$; not significant; $n = 14$; Yabby Shoals excluded). Deeper sites tended to be net heterotrophic (i.e. p/r < 1) most likely due to a combination of greater organic carbon deposition and light limitation of benthic production.

System wide annual estimates of benthic habitat metabolism

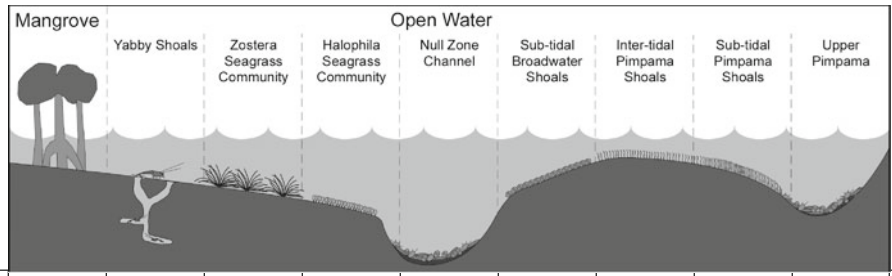
Overall, the open water benthic habitats within the study area were slightly net heterotrophic with an average O_2 p/r of 0.84 and an average TCO_2 p/r of 0.82 (Fig. 6). However, there was considerable variability in the p/r ratios of the open water habitats across the study area. For example, the *Halophila* Seagrass Communities had the highest O_2 p/r (2.30) and the 3rd highest TCO_2 p/r (1.55) and 5th largest area which, when combined, produced the largest net source of carbon for the open water habitats. The Yabby Shoals had the lowest net O_2 and TCO_2 p/r (0.39 and 0.14 respectively) which, combined with a large areal extent of 5.4 km^2, resulted in this habitat being the largest net sink of carbon. Although the *Zostera* Seagrass Communities produced the largest amount of organic matter and had the 4th largest areal extent, their high respiration rates meant that they were only a small carbon sink. The mangroves were net autotrophic and when the estimated mangrove contribution of carbon was added to the net heterotrophic open water habitat contribution of carbon the metabolism of the whole study area was in near balance (Table 3).

Carbon standing stock for the study area

Mangroves were the largest store of carbon in the study area by an order of magnitude (Table 3). The sediments contained about 1/20 the carbon stored in the mangroves and very little carbon was stored in the seagrass, water column, BMA or phytoplankton. Dividing the carbon stored in the biological pools by their respective primary production rates gives turnover times of 15.6 years for the mangroves, 16.7 days for the seagrass communities, 2.5 days for benthic microalgae and 0.8 days for phytoplankton.

Carbon budget for the study area

Carbon inputs to the study area were clearly dominated (by an order of magnitude) by primary production (carbon fixation) by mangroves, seagrass, phytoplankton and benthic microalgae (Table 3). The total open water production (5949.7 ± 1424.6 t C) was similar to the estimated mangrove production (7165.6 ± 7165.5 t C). Based on TCO_2 fixation, seagrass communities were the largest open water source of carbon to the study area (2736.8 ± 446.0 t C) and benthic microalgae the second largest (1973.4 ± 562.2 t C). Part of the seagrass productivity measurements includes production by BMA (and epiphytes) and as such BMA were probably the largest contributor of carbon to the study area (see "Discussion"). There was a net input of carbon to the study area from the Broadwater but this was not distinguishable from zero due to the large accumulation of errors. The remaining sources (diffuse sources, atmospheric deposition) contributed a much



Processes										Open Water Total	Study Area Total
TCO_2 Gross Productivity (t C yr^{-1})	7165.5±7165.5	245.1±293.0	1944.6±284.3	792.2±161.7	43.3±4.6	1055.2±165.8	138.8±18.9	452.9±48.7	38.2±31.2	4710.3±1008.1	11875.8±8173.6
TCO_2 Respiration (t C yr^{-1})	5589.1±5589.1	1691.7±763.2	2051.3±691.9	510.8±98.9	54.4±10.8	1038.1±115.8	56.7±10.3	231.1±122.4	96.7±27.2	5730.8±1840.6	11319.9±7429.7
TCO_2 Net Production (t C yr^{-1})	1576.4±1576.4	-1446.7±470.2	-106.6±407.6	281.4±62.7	-11.1±6.2	17.1±50.0	82.0±8.6	221.8±73.7	-58.5±4.0	-1020.5±1083.1	555.9±2659.5
TCO_2 p/r	1.28	0.14	0.95	1.55	0.8	1.02	2.45	1.96	0.39	0.82	1.05
O_2 Gross Productivity (t C yr^{-1})	7165.5±7165.5	877.4±97.8	1804.4±270.8	871.0±93.4	56.8±4.4	1411.7±159.6	201.0±12.6	478.8±39.7	96.1±10.1	5797.2±688.4	12962.7±7853.9
O_2 Respiration (t C yr^{-1})	5589.1±5589.1	2269.0±342.6	2298.0±556.0	378.9±28.6	63.8±4.7	1358.3±132.1	123.6±8.4	246.1±22.4	165.3±14.2	6903.1±1108.9	12492.2±6698.0
O_2 Net Production (t C yr^{-1})	1576.4±1576.4	-1391.6±244.8	-493.6±285.2	492.0±64.8	-7.0±0.3	53.4±27.6	77.3±4.2	232.8±17.2	-69.2±4.1	-1105.9±648.1	470.5±2224.5
O_2 p/r	1.28	0.39	0.79	2.3	0.89	1.04	1.63	1.95	0.58	0.84	1.04

Fig. 6 System wide annual estimates of TCO_2 and O_2 gross productivity, respiration, net productivity and gross production/respiration (p/r) ratios in the open water and mangrove habitats in Southern Moreton Bay study area. O_2 production and respiration assumes RQ and PQ = 1. Mangrove values are the same for TCO_2 and O_2 because they were calculated from mangrove biomass in the study area and a mangrove biomass versus productivity relationship for Moreton Bay just north of the study area

smaller amount of carbon. Carbon loss from the study area was dominated by atmospheric exchange of dissolved inorganic carbon (CO_2) associated with benthic and pelagic open water and mangrove respiration. Open water benthic respiration was about 6.6 times higher than pelagic respiration reflecting the shallow water column (average 1.74 m) in the study area, which is consistent with other coastal systems (see Kemp et al. 1992). Most of the open water CO_2 loss to the atmosphere occurred in the *Zostera* Seagrass Communities (35%) and Yabby Shoals (29%). The next largest estimated loss of carbon was burial. Fisheries harvest only accounted for a small amount of carbon loss.

Discussion

TCO_2 and O_2 as measures of benthic metabolism (respiration, production)

Oxygen fluxes are commonly used to measure benthic metabolism (e.g. Nowicki and Nixon 1985; Rizzo et al. 1996), but can be misleading due to temporal separation of organic matter mineralisation and oxygen consumption associated with sulphate reduction, sulphide oxidation and chemoautotrophic nitrification and underestimation of high rates of production due to bubble formation. Alternatively, TCO_2 fluxes can be used to measure benthic metabolism (e.g. McGlathery et al. 2001) but, although probably a better approach, can still be misleading due to non-biogenic fluxes associated with calcium carbonate dissolution, CO_2 assimilation by chemoautotrophic bacteria, and, to a smaller extent, methane production (Ferguson et al. 2003). Combining benthic TCO_2 and O_2 fluxes can give some insight to the most likely sediment diagenetic reactions occurring and how appropriate each parameter is as a measure of benthic metabolism (Eyre and Ferguson 2002; Ferguson et al. 2003, 2007; Barron et al. 2006). All sites (except the *Halophila* Seagrass Community) had annual dark RQs < 1, which occurs when accumulated reduced equivalents (most likely sulphide) are oxidised. Oxidation of reduced sulphide is indicative of aerobic respiration with dark O_2

Table 3 Carbon budget for the Southern Moreton Bay study area

	Carbon (t year^{-1})
Inputs	
Diffuse	534.0 ± 534.0
Atmosphere	51.0 ± 51.0
Lateral	68.1 ± 68.1
Pelagic production	1239.4 ± 416.5
BMA production	1973.4 ± 562.2
Mangrove production	7165.5 ± 7165.5
Seagrass community production	2736.8 ± 445.9
Net Broadwater Exchange	1841.2 ± 5270.7
Outputs	
Pelagic respiration	867.6 ± 291.6
Benthic respiration	5730.8 ± 1840.6
Mangrove respiration	5589.1 ± 5589.9
Burial	3419.4 ± 3419.4
Fisheries	2.6 ± 2.6
Standing stocks	
Water column	58.2 ± 19.1
Sediment	6052.6 ± 949.2
Phytoplankton biomass	2.6 ± 0.6
BMA biomass	13.7 ± 13.7
Mangrove biomass	111732.8 ± 111732.8
Seagrass biomass	125.6 ± 125.6

consumption most likely enhanced by infauna bio-irrigation (Ferguson et al. 2007). An RQ > 1 occurs when reduced equivalents are stored (most likely sulphides stored via sulphate reduction). The *Halophila* Seagrass Community had a high TCO_2 p/r suggesting that much of the organic matter driving sulphate reduction is derived from benthic production. As such, TCO_2 appears to be a better measure of the annual net benthic respiration for the open water habitats as O_2 fluxes over-estimate respiration at sites with sulphide oxidation and under-estimate respiration at sites with high sulphate reduction rates. Annually there was about a 17% difference in the TCO_2 and O_2 estimates of benthic respiration for the open water habitats (assuming RQ = 1).

Dark TCO_2 effluxes and dark RQs across the open water benthic habitats were well correlated ($r^2 = 0.68$; $p < 0.05$; $n = 14$; *Zostera* Seagrass Communities and Yabby Shoals in summer excluded) and this relationship shows that the sediments are unable to decompose organic matter via aerobic pathways once the

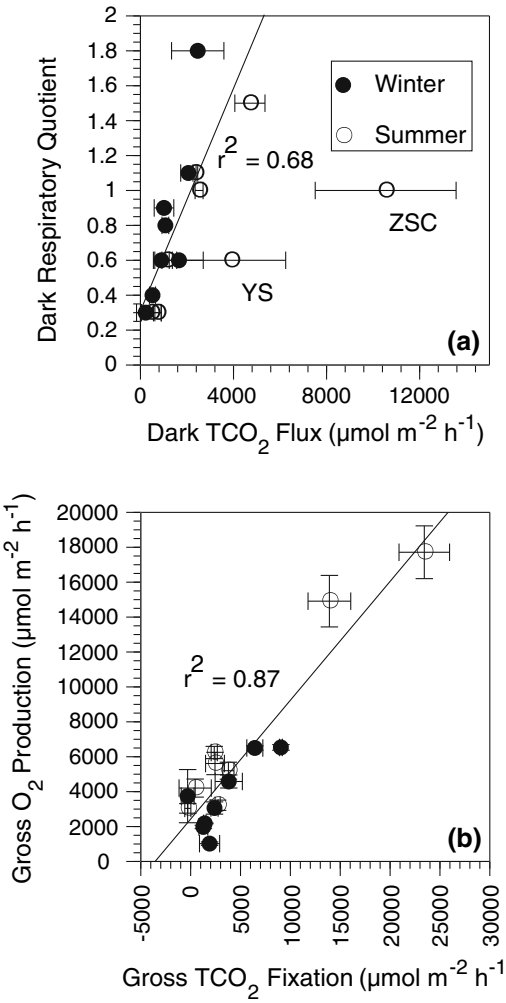


Fig. 7 **a** Dark TCO_2 fluxes (respiration) as a function of dark RQ (mean ± SE; $n = 3$) and **b** gross CO_2 fixation as a function of gross O_2 productivity (mean ± SE; $n = 3$), in the eight open water benthic habitats. *ZSC Zostera* Seagrass Community, *YS* Yabby Shoals

respiration rates exceed about 2,200 µmol TCO_2 m^{-2} h^{-1} (Fig. 7a). This same aerobic/anaerobic threshold was found in the sub-tropical Brunswick Estuary (Eyre and Ferguson 2005). The two outliers were the Yabby Shoals and *Zostera* Seagrass Community in summer, which had much higher dark TCO_2 fluxes for a given dark RQ indicating that these habitats were able to maintain very high aerobic respiration rates. Yabbies and seagrasses are both able to translocate oxygen from the surface into the sediments (Webb and Eyre 2004a; Frederiksen and Glud 2006), which may facilitate aerobic respiration even under high organic matter loadings.

Gross TCO_2 fixation and gross O_2 production rates across the open water benthic habitats were well correlated ($r^2 = 0.87$; $p < 0.0001$; $n = 16$) with a phytosynthetic quotient (PQ) of 1.25 (Fig. 7b), which falls within the expected range of 1.0–1.6 depending on the source of nitrogen (nitrate or ammonium) and type of carbon produced (carbohydrate or lipid synthesis; Eyre and Ferguson 2002). The measured PQ would be expected to fall outside the 1–1.6 range if there had been significant $CaCO_3$ precipitation or sulphide oxidation associated with autotrophic production (Eyre and Ferguson 2002; Ferguson et al. 2003; Cook et al. 2004). The relationship between light (net) TCO_2 fixation and light (net) O_2 production rates across the open water benthic habitats was similar to the gross rates ($r^2 = 0.80$; $p < 0.001$; $n = 16$), with a photosynthetic quotient (PQ) of 1.23 indicating that correction of net benthic production for respiration to calculate gross production was consistent across the study area. The seagrasses contrast with other studies where TCO_2/O_2 net benthic production ratios have been shown to vary between 0.3 and 4.8 in *P. oceanica* communities (Barron et al. 2006) and from 0.6 to 6.8 in *T. testudium* communities (Ziegler and Benner 1999). Overall, in this system both TCO_2 and O_2 appear to be a good measures of the annual net production with only an 8% difference for the open water habitats (assuming PQ = 1).

Seagrass habitats

Seagrasses are often seen as 'iconic' habitats and are the only benthic habitats considered in many assessment, protection and restoration efforts. Much of the value of seagrass is associated with their 3-dimensional habitat, which provides refuge for animals (Hosack et al. 2006), enhances species diversity (Connolly 1994) and provides a surface for algae to colonise (Hauxwell and Valiela 2004). The contribution of seagrasses to food webs or net ecosystem metabolism is generally of lesser importance (Hemminga and Duarte 2000; Santos et al. 2004). Similarly, in southern Moreton Bay the *Zostera* Seagrass Communities also made little contribution to the net ecosystem metabolism with a p/r of 0.95 (based on TCO_2 fixation). Net heterotrophic metabolism was in contrast to many seagrass communities that are net autotrophic (e.g. Murray and Wetzel 1987; Ziegler and Benner 1999; Gazeau et al. 2005 and also reviews Gattuso et al. 1998; Hemminga and Duarte 2000) or in near balance (e.g. Santos et al. 2004) and most likely reflects the age of the *Zostera* Seagrass Communities in southern Moreton Bay. Aerial photographs show that these seagrass beds have been stable for over 30 years (SKM 2006). As seagrass communities age there is an associated increase in net heterotrophy driven by an input and trapping of organic material in the canopy (Barron et al. 2004). In contrast, the *Halophila* Seagrass Communities had a p/r of 1.55 (based on TCO_2 fixation) and contributed 47% of the net production to the study area (Fig. 6). This probably reflects the rapidly growing and decaying (ephemeral) nature of the *Halophila* Seagrass Communities compared to the more stable *Zostera* Seagrass Communities.

Despite having high gross and net productivities other components of seagrass communities, such as epiphytes and benthic microalgae, can make up the bulk of the gross production. For example, gross production (TCO_2 fixation) by benthic microalgae on the Sub-tidal Broadwater Shoals without seagrass was on average 27 and 35% of the gross production on the Sub-tidal Broadwater Shoals with *Zostera* and *Halophila*, respectively, suggesting that seagrass and epiphytes combined contribute about 65–73% of the total gross benthic productivity. This is similar to a *Halodule wrightii* seagrass community in Mississippi Sound which contributed 77% to total gross benthic productivity, of which only 17% was contributed by the seagrasses themselves (Moncreiff et al. 1992). The remaining 60% of total benthic production was by epiphytes (Moncreiff et al. 1992). The contribution of epiphytes to total benthic production in southern Moreton Bay is unknown. However, assuming that seagrass contributed 17%, and benthic microalgae 27 and 35%, of the gross productivity in *Zostera* and *Halophila* communities respectively, epiphytes would contribute the remaining 56 and 48%. Using these gross productivity estimates, benthic microalgae could produce the largest amount of carbon for the open water (2775.7 t), epiphytes could produce the second largest amount (1469.3 t), phytoplankton the third largest amount (1239.4 t) and seagrass the smallest amount (465.3 t). Caution needs to be applied to these estimates as differences in the canopy structure between the Halodule communities in the Moncreiff et al. (1992) study and the *Zostera* and *Halophila* communities in this study would

influence light attenuation, hydrodynamics, nutrient availability and grazing, making direct comparisons difficult. However, these rough estimates give some insight into the potential importance of benthic microalgae and epiphytes to the carbon budget of this open water benthic system and highlight an area for further research.

Non-seagrass benthic habitats—importance of spatial replication

The most important outcome of this study is the finding that shallow subtropical coastal systems have a complex mosaic of benthic habitats and some of these less 'iconic' habitats also make an important functional contribution to the whole ecosystem. For example, the largest amount of net respiration occurred in Yabby Shoals. Higher respiration rates associated with yabbies are mostly due to increased microbial respiration associated with organic matter enrichment and increased surface areas of their burrows, with a small amount due to the animal (Webb and Eyre 2004a). In addition, permeable sandy sediments in the absence of the burrowing shrimp, *Trypaea australiensis* can also have significant rates of organic matter mineralisation (Cook et al. 2007; Glud et al. 2008). In other studies of benthic metabolism in vegetated open water coastal systems only 'vegetated' and 'unvegetated' habitats are usually included (e.g. Ziegler and Benner 1999; Gazeau et al. 2005; Barron et al. 2006) which could result in a misinterpretation of net metabolism. For example, if the Yabby Shoals had not been included in our benthic measurements the net metabolism (p/r) of the open water benthic system would have changed from net heterotrophic (p/r = 0.82) to net autotrophic (p/r = 1.11). This highlights the importance of benthic habitat mapping and spatial replication to capture all the benthic habitats, not just the 'iconic' ones and 'others' when assessing the metabolism of coastal systems.

Some of the muddy non-seagrass habitats also had some of the highest gross and net productivities in the study area (Fig. 6) clearly highlighting the importance of these less 'iconic' habitats to the overall system productivity. For example, although the Pimpama Sub- and Inter-tidal Shoals only cover about 10% of the open water area they accounted for 50% of the open water net benthic production. It is unknown why these habitats had high net productivities compared to the other non-seagrass habitats, which had an almost balanced metabolism (Fig. 6). One possibility is that nutrient inputs from the Pimpama River are driving the high net productivities, as this nitrogen load (Eyre et al. 2010) can account for around 100% of the net production. N-fixation in these habitats is unimportant. Alternatively, the differences in net production may be related to differences in the type of benthic microalgae (BMA) within the different habitats. Unfortunately the BMA were not identified under the microscope, but visually there were distinct differences with a more filamentous algae at the sub- and inter-tidal Pimpama habitats.

Overall gross benthic production rates in the non-seagrass habitats were low compared to other systems. In a compilation of 85 shallow polar to tropical coastal systems benthic production rates ranged from 8 to 48 mol C m^{-2} $year^{-1}$ for sub-tidal and inter-tidal sediments (Cahoon 1999) and in a compilation of 20 shallow mostly temperate coastal systems benthic production rates ranged from 4 to 26 mol C m^{-2} $year^{-1}$ for inter-tidal sediments (Underwood and Kromkamp 1999). The sub-tidal and inter-tidal Pimpama Shoals were the most productive non-seagrass benthic habitats in Southern Moreton Bay, but the rates measured (10.5–13.7 mol C m^{-2} $year^{-1}$) were at the lower end of the range reported for other systems. Similarly, benthic chlorophyll-a concentrations were also very low compared to other systems (Cahoon 1999; Underwood and Kromkamp 1999). Low sediment chlorophyll-a concentrations in southern Moreton Bay may reflect grazing pressure as the benthic microalgal biomass was observed to increase rapidly in cores when grazing pressure was mostly removed.

Benthic habitat connectivity

TCO_2 p/r of the open water benthic habitats varied widely across the study area ranging from 0.14 to 2.45, but when weighted by habitat area the overall open water benthic system p/r was slightly net heterotrophic (0.82) and was in near balance across the whole system (1.04). With such a wide range of habitats in close proximity it is expected that habitats are strongly connected due to the large tidal flows of water across the study area; the entire study area is flushed each tidal cycle (Szylkarski et al. 2005; SKM 2006). The net autotrophic habitats (e.g. *Halophila*

Seagrass Communities; Mangroves) are likely to be a source of organic matter for the net heterotrophic habitats (e.g. Yabby Shoals) and the net heterotrophic habitats are likely to be a source of nutrients for the net autotrophic communities. Interestingly, the net production by Mangroves (1576.4 t) was similar to the net respiration in the Yabby Shoals (1446.7 t). The *Zostera* Seagrass Community may also be a source of dissolved organic nitrogen (and associated dissolved organic carbon) for the Yabby Shoals (Eyre et al. 2010). This strong connectivity across a mosaic of benthic habitats, and across the study area boundaries (see later "Discussion"), and the associated transport of organic matter and nutrients would help relieve resource limitation and maintain higher primary and secondary production (Cloern 2007). Further work on the connectivity between these different habitats is required.

Benthic versus pelagic production

The ratio of open water benthic production to open water total production was 0.82 (O_2 production) to 0.79 (TCO_2 fixation). This is at the higher end of the range of the ratios reported for subtropical coastal systems (0.28–0.92; see Moncreiff et al. 1992). The high ratio of benthic to total production reflects a combination of the average shallow depth of the study area (1.74 m) and low water column nutrient and phytoplankton biomass concentrations (see Table 2); dry season algal biomass (chlorophyll-a) concentrations in the Broadwater average 1.6 μg l^{-1} and DIN concentrations average 1.1 μmol l^{-1} (Eyre et al. 2010). The shallow water depth reduces the volume of water for pelagic production and increases the amount of light available for benthic production. In addition, much of the nitrogen and phosphorus in the study area was stored in the sediments (Eyre et al. 2010) and the benthic primary producers are able to access these nutrients, giving them a competitive advantage over phytoplankton. The benthic producers also intercept nutrients fluxing across the sediment-water interface, making them unavailable to phytoplankton. Further, the rapid tidal flushing of most of the study area (<1 day) is less than the doubling time of phytoplankton.

The open water ratio of benthic to total production did not change (0.79) from winter to summer if TCO_2 fixation rates are used and only changed from 0.81 in winter to 0.83 in summer if O_2 production rates are used. This minor seasonal change in benthic to total production contrasts with temperate systems where there is a much larger seasonal variation (McGlathery et al. 2001) and reflects the similar change in both compartments between summer and winter. Following floods however, diffuse loads of dissolved inorganic nitrogen from the catchment can stimulate phytoplankton growth in the Coomera and upper Pimpama river estuaries with recorded chlorophyll-a concentrations up to 57.2 and 33.1 μg l^{-1}, respectively. Flood events can also be immediately followed by decreases in benthic production due to scouring of the sediment surface (Eyre and Ferguson 2006). In the current study, the areal extent of *Halophila* Seagrass Communities also decreased following flooding (SKM 2006). These episodic changes in pelagic and benthic production were not fully captured by the process measurements and budgeting used in this study and as such, the benthic production to total production ratio should be considered a dry season ratio.

Budget uncertainty and balance

The C budget was constructed using a combination of measured open water benthic metabolism rates scaled up to the whole study area, measured biomass and biomass versus productivity relationships (i.e. pelagic production, mangrove production), modelled fluxes (e.g. catchment loads) and literature values (e.g. burial rates). Errors were estimated for each of the budget terms and the sensitivity of the budget to each of these errors was tested. However, the error analysis does not account for spatial and temporal variability in benthic metabolism measurements that was not captured by the limited replication (particularly temporal replication) and does not indicate how relevant the literature values are to the study area. We erred on the side of caution by assigning 100% error to modelling and literature values but, obviously, large uncertainties associated with the budgets remain. This is particularly the case for the Broadwater exchange term that includes the sum of the errors associated with all the other components of the budget. Uncertainty is also a particular problem for net ecosystem metabolism estimates, because the large productivity and respiration rates with associated large errors are in near balance (Smith and Hollibaugh 1997). We were unable to use PO_4^{3-} budgets (i.e. LOICZ; Gordon et al. 1996)

to estimate NEM due to the lack of a salinity gradient across the study area (Table 2). Despite these uncertainties we still considered it better to make some rough approximations to illustrate potential important fluxes and processes in an oligotrophic sub-tropical coastal system than not make the budget calculations at all. The C budget should be considered in this context. Some of the important uncertainties and their impacts on the C budget are discussed below.

Although this study involved a detailed assessment of spatial variability in benthic metabolism (i.e. triplicate measurements in each major benthic habitat), the rates were only measured in summer and winter. A major assumption made when constructing the carbon budget was that summer and winter measurements were sufficient for scaling up to an annual budget. Subtropical coastal systems do not have the distinct four seasons typical of temperate systems, and maximum benthic productivity and respiration typically occurs in summer, and minimum benthic productivity and respiration typically occurs in winter (Eyre and Ferguson 2005). As such, averaging summer and winter benthic productivity and respiration rates should give a reasonable estimate of average rates that can be scaled up to an annual budget. To test this assumption the data set from Eyre and Ferguson (2005) was used to calculate benthic productivity and respiration rates using (1) monthly data over 2 years and (2) just using the summer and winter rates. Annual benthic respiration estimates determined by the two approaches differed by only 13% and annual benthic productivity estimates differed by only 26%. Adding the potential magnitude of temporal error to the spatial error associated with the open water net benthic production estimates (-1105.9 ± 648.1 t C; Fig. 6) would still allow the open water benthic system to be distinguished as net heterotrophic.

Import of organic matter is required to support a heterotrophic open water benthic system. Our estimates suggest that it is unlikely that the combined terrestrial, atmospheric and lateral inputs of organic matter would be sufficient to cause net heterotrophic metabolism in the open water benthic system (Table 3). It is also unlikely that net pelagic production within the study area alone would be sufficient, but when combined with the inputs of organic matter from the terrestrial, atmospheric and lateral sources and associated errors these sources may be large enough to drive net heterotrophic metabolism in the benthic system (Table 3). Similarly, our estimates suggest that the load of organic matter from net mangrove production would provide enough organic matter to drive net heterotrophic metabolism in the open water benthic system. However, none of these estimates have included burial within the open water benthic system and mangroves. Including our estimates of burial results in the C budget having a deficit of 1841.2 ± 5270.7 t C (based on CO_2 fluxes), which requires an import of C to the study area across the Broadwater boundaries to balance (Table 3).

The error associated with Net Broadwater Exchange includes the sum of the errors associated with all the other terms of the budget and is therefore large, making it difficult to distinguish the Net Broadwater Exchange from zero. Most of this Broadwater exchange error is due to the large errors assigned to the burial rates ($\pm 100\%$) and the mangrove metabolism ($\pm 100\%$). This is reflected in the sensitivity analysis, which showed that the amount of carbon exported across the Broadwater boundaries was most sensitive to the burial rates and mangrove metabolism (Table 4). However, applying a range of net mangrove productions from zero to double the budget estimates still requires a net import of organic matter to the study area to balance the C budget (Table 4). Similarly, burial rates would need to be reduced to less than 50% of the budget estimates to change the overall conclusion of the C budget (Table 4) but we see no reason why this system should have particularly low C burial rates. An import of organic matter is also consistent with net autotrophy (i.e. export of organic matter) in Moreton Bay (Eyre and McKee 2002) which joins the northern boundaries of the study area. Measured burial rates are clearly required to better constrain the C budget of southern Moreton Bay.

Although somewhat speculative, there is also some additional evidence to suggest the C budget deficit may be real. Nitrogen and phosphorus budgeting, which was based on independent measurements, also showed that an import to the study area across the Broadwater boundaries was required to balance the budgets (Eyre et al. 2010). The molar ratios of the carbon, nitrogen and phosphorus deficits was reasonably similar to Redfield (73:18:1) given the associated errors in the estimates, suggesting phytoplankton as a possible source of the organic material imported into the study area. Because it is unlikely that the

Table 4 Sensitivity analysis for the southern Moreton Bay carbon budget

Carbon budget term adjusted	Net Broadwater Exchange (t year^{-1})	
	Error adjusted down	Error adjusted up
Diffuse	2375.2	1307.2
Atmosphere	1892.2	1790.2
Lateral	1909.3	1773.1
Pelagic production/respiration	1966.1	1716.3
Benthic production/respiration		
Sub-tidal Broadwater Shoals	1891.2	1791.2
Yabby Shoals	1371.0	2311.4
Sub-tidal Pimpama Shoals	1464.8	2217.6
Upper Pimpama	1935.2	1747.2
Inter-tidal Pimpama Shoals	1798.7	1883.7
Null zone channel	1845.2	1837.2
Zostera Seagrass Community	1849.8	1832.6
Halophila Seagrass Community	1835.0	1847.4
Mangrove production/respiration	3417.6	264.8
Burial	−1578.2	5260.6
Fisheries	1838.6	1843.8

Each input and output term was adjusted up and down by its associated error to determine how these errors influenced the budget deficit/surplus (Net Broadwater Exchange—input)

C:N:P import ratio was similar to Redfield by coincidence, the independently estimated N and P fluxes suggest that the flux of imported C is a reasonable estimate (convergence of estimates). Seagrasses are known to trap phytodetritus (Gacia et al. 2002) suggesting the extensive seagrass beds may trap phytoplankton as large tidal volumes of water move through the study area. The net heterotrophic metabolism in the *Zostera* seagrass habitat is consistent with an import of organic material. Trapping of phytoplankton would be enhanced in the Null Zone Channel where oceanic water flowing in from Jumpinpin and Moreton Bay (north) and the Gold Coast Seaway (south) meet (Fig. 1; SKM 2006). Hydrodynamic modelling showed this was a low tidal energy area, and this results in the deposition of muds and phytodetritus (visual observation). Applying the average total organic carbon: total phosphorus mass ratio in the Moreton Bay water column (39.1; Eyre and McKee 2002) to the total annual phosphorus input across the Broadwater boundaries determined using hydrodynamic modelling (874.0 t; Szylkarski et al. 2005; SKM 2006) gives a total annual carbon input of 34,173.4 t. As such, the net input of carbon via trapping of phytoplankton that is required to balance the budget is only 5 ± 15% of the total tidal carbon input, which appears reasonable.

Whole system budget comparisons

Similar to other mangrove-lined tropical systems (e.g. Darwin Harbour, Australia: Burford et al. 2008; Hinchinbrook Channel, Australia: Alongi et al. 1998; Sawi Bay, Thailand: Alongi et al. 2000) mangrove production in southern Moreton Bay was the largest source of primary production. But annual estimates of gross primary production, respiration and net ecosystem metabolism were much lower than in the tropical systems, even with similar percentage coverage of mangroves (Table 5), probably reflecting the reduced sub-tropical growing climate. Mangroves have a larger areal extent in southern Moreton Bay than the whole of Moreton Bay (as defined in Eyre and McKee 2002) (Table 5), which is also reflected in their C budgets. For example, pelagic production was the largest source of C in the whole of Moreton Bay due to the greater percentage area of open water and deeper water column (Eyre and McKee 2002). Despite a similar coverage (Table 5), seagrass contributed a much larger percentage of gross primary production in southern Moreton Bay (26%) than the whole of Moreton Bay (7%). These differences are mostly due to differences in the methods used to estimate seagrass production. In southern Moreton Bay estimates are based on seagrass community

Table 5 Comparison of whole system metabolism estimates for tropical and subtropical coastal systems with seagrass and mangroves

System	Climate zone	Mangrove (%)	Seagrass (%)	GPP (mol C m^{-2} $year^{-1}$)	R (mol C m^{-2} $year^{-1}$)	GPP/R (mol C m^{-2} $year^{-1}$)	NEM	Source
Darwin Harbour[a]	Tropical	18		137	66	2.1	+93	Burford et al. (2008)
Hinchinbrook Channel[a]	Tropical	36		391	195	2.0	+31	Alongi et al. (1998)
Mantang Forest[a]	Tropical	20		370	264	1.4	+18	Alongi et al. (2000)
Sawi Bay[a]	Tropical	67		578	412	1.4	+21	Alongi et al. (2004)
Southern Moreton Bay (open water benthic system)	Subtropical	0	24	20	24	0.8	−4	This study
Southern Moreton Bay (open water system)	Subtropical	0	24	25	27	0.9	−2	This study
Southern Moreton Bay (including mangroves)	Subtropical	43	13	29	27	1.1	+2	This study
Moreton Bay	Subtropical	6	12	24	22	1.1	+2	Eyre and McKee (2002)
Laguna Madre (open water benthic system)	Subtropical	0	75	57	43	1.3	+14	Ziegler and Benner (1999)
Laguna Madre	Subtropical	0	75	59	51	1.2	+17	Ziegler and Benner (1999)
State Park[b]	Subtropical	0	65	36	18	2.0	+12	Stutes et al. (2007)
Kee's Bayou[b]	Subtropical	0	4	19	9	2.1	+15	Stutes et al. (2007)

[a] Compiled in Burford et al. (2008)

[b] Daily rates × 365 to make annual estimates

production (i.e. includes epiphytes and benthic microalgae), but in the whole of Moreton Bay they were based on seagrass growth rates (Dennison et al. 1999). Using the revised estimates of seagrass production (465.3 t C see "Discussion") southern Moreton Bay seagrasses only contributed 4% of the gross primary production which is much closer to the whole of Moreton Bay estimates.

Despite differences in the compartments of production southern Moreton Bay and Moreton Bay had similar whole system rates of annual gross primary production, respiration and net ecosystem metabolism and similar gross primary production/respiration (Table 5). However, the open water benthic system and open water system had lower rates of gross primary production, respiration and NEM and were more heterotrophic than other coastal systems with seagrass (Table 5). Two associated factors may explain the heterotrophic status of southern Moreton Bay. Firstly, the unique system hydrodynamics where oceanic water flowing in from Jumpinpin and Moreton Bay (north) and the Gold Coast Seaway (south) meet, resulting in the import and deposition of organic matter, would drive net heterotrophic metabolism in the system. Lateral exchanges of carbon have been shown to be important in a number of types of coastal ecosystems (Smith and Hollibaugh 1997; Neubauer and Anderson 2003; Bouillon et al. 2007) and as such, are important for determining their metabolic status and gaseous exchange with the atmosphere (Duarte and Prairie 2005). Coastal systems that receive inputs of terrestrial organic matter are typically net heterotrophic because this material has a high C/N resulting in a low release of nutrients during decomposition compared to phytodetritus. This is at odds with the import of low C/N phytoplankton driving net heterotrophy in the study area, but can be explained by the large loss of nitrogen via high rates of denitrification in the seagrass habitats (Eyre et al. 2010). Secondly, this study captured the metabolism of all the major benthic habitats and did not lump all the habitats other than seagrass together as 'unvegetated'. As previously demonstrated, by excluding just one of these habitats (e.g. Yabby Shoals) the metabolic status of the system would change to net autotrophic. As such, differences in the benthic habitat mapping and spatial replication between this study and previous studies in coastal systems with seagrass (Table 5) may explain differences in the NEM. In addition, our chambers were designed to capture the passive flow through *T. australiensis* burrows (see Webb and Eyre 2004b) highlighting the need to use appropriate techniques when assessing benthic metabolism of benthic habitats with large burrowing macrofauna.

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